

Effects of stand tending on the estimation of aboveground biomass of planted juvenile white spruce

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Abstract: Stem, branch, needle, and total aboveground biomass were assessed for three 9- to 12-year-old white spruce (*Picea glauca* (Moench) Voss) plantations, each subjected to three different stand tending options at age 4 to 7. Biomass components were predicted from measures of stem diameter with coefficients of variation between 24% and 29%. Diameter at breast height (DBH) generally provided lower prediction precision than did the lower stem measures tested (coefficient of variation > 35%). The addition of tree height in models reduced the standard error of the estimates for stem and total biomass by an average of 48% and 8%, respectively, and compensated for different height/diameter ratios imposed on the spruce by the stand tending treatments. Needle and branch biomass models were invariant to the tending treatments and, consequently, to the addition of height as an independent variable. Predictions from existing published white spruce equations suggest that extrapolation to this study area would have led to adequate stem biomass estimation but to serious (>55%) underestimates of branch, needle, and, correspondingly, total biomass. Slow self-pruning by plantation spruce, particularly before crown closure, is cited as a possible reason for these differences.

Résumé : La biomasse de la tige, des branches et des aiguilles ainsi que la biomasse épicée totale ont été évaluées dans trois plantations d'épinette blanche (*Picea glauca* (Moench) Voss) âgées de 9 à 12 ans. Chaque plantation avait été soumise à trois types de traitements culturaux entre l'âge de 4 et 7 ans. Les composantes de la biomasse ont été dérivées à partir des mesures de diamètre de la tige avec des coefficients de variation allant de 24 à 29 %. Les prédictions faites à partir du diamètre à hauteur de poitrine (DHP) avaient une précision moindre que celles qui reposaient sur les autres mesures qui ont été testées plus bas sur la tige (coefficient de variation > 35 %). L'addition de la hauteur des arbres dans les modèles a réduit l'erreur type des estimations de la biomasse de la tige et de la biomasse totale par respectivement 48 et 8 % en moyenne et compensé les différences dans le rapport entre la hauteur et le diamètre provoquées chez l'épinette par les traitements culturaux. Les modèles de biomasse des aiguilles et des branches n'étaient pas affectés par les traitements et, par conséquent, par l'ajout de la hauteur comme variable indépendante. Les prédictions faites à l'aide des équations existantes publiées pour l'épinette blanche indiquent que l'extrapolation à cette zone d'étude aurait fourni une estimation adéquate de la biomasse de la tige, mais aurait entraîné une importante sous-estimation (>55 %) de la biomasse des branches et des aiguilles et, par voie de conséquence, de la biomasse totale. La lenteur de l'élégage naturel dans les plantations d'épinette, particulièrement avant la fermeture du couvert, serait possiblement une raison pour expliquer ces différences.

[Traduit par la Rédaction]

Introduction

The Fallingsnow research area was established in 1993 to study the effects of an array of conifer release options on a white spruce (*Picea glauca* (Moench) Voss) – trembling aspen (*Populus tremuloides* Michx.) boreal mixedwood ecosystem (Bell et al. 1997). Since this time, additional research efforts have been undertaken at Fallingsnow, ranging from quantifying vegetation response (Bell and Newmaster 2002; Newmaster and Bell 2002) to assessing treatment effects on

growing resources (Reynolds et al. 2000a, 2000b). More recently, ongoing research efforts aimed at quantifying tree nutrition, productivity, nutrient cycling, carbon sequestration, and growth and yield responses have generated demands for biomass estimates for the planted spruce.

The application of existing equations offers the most economical solution to any biomass estimation need and was considered for Fallingsnow. However, the potential for bias in a particular situation must be carefully weighed against the cost of calibrating existing equations or constructing new ones (Crow and Schlaegel 1988). Generalized biomass equations have been produced for most tree species in North America (e.g., Jenkins et al. 2003) and are intended for estimates that average across a variety of conditions. Unfortunately, they cannot be expected to produce bias-free estimates for a particular set of conditions, such as those at Fallingsnow. Alternatively, several biomass studies have specifically included white spruce (Baskerville 1965; Ker 1980; Ker and van Raalte 1981; Lavigne and van Nostrand 1981; Freedman et al. 1982; Alemdag 1983; Singh 1984), but few

Received 22 April 2003. Accepted 24 September 2003.
Published on the NRC Research Press Web site at
<http://cjfr.nrc.ca> on 22 March 2004.

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were based on sampling in plantations (Harding and Grigal 1985) and juvenile stands (Ter-Mikaelian and Parker 2000). Moreover, only the latter study addressed potential influences of stand tending treatments on biomass relationships, and results were somewhat inconclusive. Thus, without being able to quantify bias associated with differences in factors such as site, tree size, and stand conditions (e.g., age, site quality, history, etc.), we felt it necessary to construct a set of biomass equations specifically for the plantation spruce encompassed by the Fallingsnow research area.

The objectives of this investigation were twofold: (1) to report equations for predicting juvenile foliage, branch, stem, and total aboveground biomass for spruce at Fallingsnow, and (2) to examine the effects of stand tending on these biomass relationships. While we agree with the extrapolation cautions identified by Crow and Schlaegel (1988), we also recognize that it may not be practical to develop biomass prediction equations for every circumstance. This paper will address whether or not, in such cases, it may be prudent for foresters and researchers to account for different stand tending histories when applying these or other biomass equations to similar circumstances.

Materials and methods

Study area

The Fallingsnow Ecosystem Project is located in Fraleigh Township (48°08'N, 89°49'W), approximately 60 km southwest of Thunder Bay, Ontario. The area is characterized by productive, fine-textured soils typical of mixedwood sites bordering the Boreal and Great Lakes – St. Lawrence forest regions. Prior to harvest, 75-year-old trembling aspen and white spruce dominated the area. Three representative blocks, each at least 50 ha, were clear-cut harvested between 1986 and 1988, site prepared mechanically, and planted to white spruce between 1989 and 1990 (Bell et al. 1997). Broadcast release treatments, including motor-manual cutting and the herbicide glyphosate (formulated as Vision® by Monsanto Canada Inc.), were applied at the end of the 1993 growing season. Treatments, including an untreated "control", were randomized within each of the three blocks, based on a randomized complete block design.

Biomass determinations

A total of 15 planted white spruce were selected for aboveground biomass sampling from within each plot of the control, herbicide, and brushsaw treatments in each of the three blocks. Each set of trees in a plot was chosen to reflect an even distribution throughout the full range of tree heights documented for that plot. In addition to meeting these height conditions, selected trees were of good form and free from obvious mechanical, insect, or other defects. On 10–14 May 1999, the identified trees were measured for total height (HT, cm), maximum stem diameter (D_1 , cm), and diameter at 90° to maximum (D_2 , cm) and at 0 (groundline), 10, 15, 30, and 137 (DBH) cm above groundline, maximum crown diameter (CD_1 , cm), and crown diameter at 90° to maximum (CD_2 , cm). The five measures of stem diameter (D_0 , D_{10} , D_{15} , D_{30} , and DBH) were selected to reflect various measures frequently used in studies of juvenile stands.

Immediately following measurement, the selected trees were severed at groundline, carried to roadside, and bagged in plastic netting. Harvested trees were placed in shaded areas and transported to Sault Ste. Marie on 14 May. Upon arrival at the Ontario Forest Research Institute, the trees were placed in frozen storage until drying. Initial drying took place at 30–40 °C, until needles separated freely from the branches and stem. Branches and needles were then bagged separately, and all three components (needles, branches, and stem) were oven-dried at 71 °C to a constant mass. Masses were recorded to the nearest 0.1 g for each tree.

Data analysis

In preparation for biomass equation construction, pairs of raw stem and crown diameter measurements were averaged using the formula for the geometric mean:

$$[1] \quad D = \sqrt{D_1 \times D_2} \quad \text{and} \quad CD = \sqrt{CD_1 \times CD_2}$$

where D is the stem diameter, CD is crown diameter, and D_i or CD_i are the raw measurements as defined above. Scatterplots and simple correlations were then constructed for all meaningful combinations of potential dependent and independent variables, including their natural log transformed values.

The basic allometric equation for biomass was the first model fit to the data:

$$[2] \quad M = \beta_0 D^{\beta_1}$$

where M represents a measure of biomass, β_0 and β_1 are parameters to be estimated, and D is one of the measures of stem diameter. When variance in biomass increased with stem diameter, the multiplicative-error form of this model was assumed (Baskerville 1972) and the parameters β_0 and β_1 were estimated using ordinary least squares on the natural log transformed model:

$$[3] \quad \ln(M) = \ln(\beta_0) + \beta_1 \ln(D) + \ln(\epsilon)$$

When variance in biomass remained constant across the range of stem diameters, the additive-error form of the model was fit using nonlinear regression methods:

$$[4] \quad M = B_0 D^{B_1} + \epsilon$$

In either case, model residuals were examined to ensure that regression assumptions were met (Draper and Smith 1981).

Once a suitable model was obtained for each biomass component and each stem diameter measure, the relationships were tested for treatment effects by fitting the models individually to the data from each plot and using the resulting parameter estimates for β_0 and β_1 , b_0 and b_1 , as raw data in analyses of variance (ANOVA) that incorporated the underlying randomized blocks experimental design. Multivariate F tests (Wilk's Lambda) were used to account for correlations between the two parameters, with orthogonal contrasts to compare the relationships of treated versus control and herbicide-treated versus manually treated plots. Standard errors for the parameter estimates reported for eqs. 3 or 4 were obtained directly from the analyses of variance (i.e., $SE = [(MSE)/N]^{1/2}$, where $N = 3$, the number of blocks used to obtain the estimate). In this manner, the reported standard errors reflect block-to-block variation, and

precision is not artificially inflated by the number of trees involved in the regressions.

Next, we attempted to improve upon the stem-diameter-only regressions and (or) produce more robust regressions that accounted for unexplained treatment variation present in eqs. 3 or 4 by adding the independent variables HT and CD to the prediction equations. Equation 2 was expanded to

$$[5] \quad M = \beta_0 D^{\beta_1} HT^{\beta_2} CD^{\beta_3}$$

and insignificant predictor variables were removed through backwards elimination ($\alpha = 0.05$). Height and diameter are often combined as a volume index for biomass prediction (Crow and Schlaegel 1988), and so the variation

$$[6] \quad M = \beta_0 (D^2 HT)^{\beta_1} CD^{\beta_2}$$

was tested in a similar manner. With those relationships characterized by constant variance in biomass across the predictor variables, additional nonlinear models were tested, including the monomolecular function (Draper and Smith 1981) and a modification of Honer's standard volume equation (Lavigne and van Nostrand 1981; Honer et al. 1983):

$$[7] \quad M = \beta_0 + \frac{D^{\beta_1}}{\beta_2 - (\beta_3/HT)} + \epsilon$$

The models were compared on the basis of goodness of fit, using model statistics including the RMSE (root mean square error, or standard error of the estimate), coefficient of determination (R^2), significance of parameters, and residual plots. For comparative convenience, parameter estimates generated for log-linear models were back transformed to arithmetic units, and predicted values were corrected for bias using the following correction factor (Baskerville 1972):

$$[8] \quad CF = e^{(MSE/2)}$$

where MSE is the mean square error from the log-linear regression, and e is the Euler constant (2.7183). For example, predictions made from eq. 3 would be computed, in arithmetic units, according to

$$[9] \quad \hat{M} = (b_0 D^{b_1}) CF$$

Similarly, RMSE values were translated to arithmetic units by computing the antilog of the predicted values from the log-linear model, multiplying the results by the bias correction factor, and recomputing the RMSE as

$$[10] \quad RMSE' = \sqrt{\frac{\sum_{i=1}^n (M_i - \hat{M}_i)^2}{n-2}}$$

where $RMSE'$ is the model RMSE in arithmetic units, M_i is the biomass of the i th tree in arithmetic units, $\hat{M}_i$ is the bias-corrected predicted biomass for the i th tree, from the log-linear model, and n is the number of trees involved in the regression. Where nonlinear regression was used, the coefficient of determination was estimated by

$$[11] \quad R^2 = 1 - \frac{\text{Residual sum of squares}}{\text{Corrected total sum of squares}}$$

Once the most improved models were determined, parameter estimates from the fit of each model to the data from each plot were subjected to multivariate analysis of variance to test whether the expanded models fully accounted for variation related to the tending treatments.

Application of the models to spruce at Fallingsnow

To estimate white spruce biomass on Fallingsnow plots and verify that the improved models were robust and fully accounted for treatment-related variation, the biomass equations were applied to independent sample data collected from the plots in May 2000. Within each plot, 30 clusters of five 2 m $\times$ 2 m plots were installed at random within the treated portions of the plantations (i.e., missed strips were excluded), and white spruce within these plots were measured for total height and stem diameter (D_{10}). Needle, branch, stem, and total aboveground biomass were then estimated for each tree using (1) equations based on stem diameter alone, (2) improved and (or) robust equations based on both stem diameter and height, if found, and (3) expanded stem-diameter-based equations containing different parameter estimates for each of the tending treatments. For the latter, indicator variables were used with eq. 2 to generate separate parameter estimates for each of the three treatments. Data from the three estimates for each biomass component were expressed in terms of biomass per tree and biomass per hectare. Treatment means and their standard errors were computed from analysis of variance of the plot data and compared among estimation methods.

Results

Although the target sample size for each plot was 15 trees, 16 were inadvertently sampled in one of the control plots, and only 14 were sampled in one of the brushaw plots (Table 1). Basal diameters ranged from 1.6 to 11.4 cm; total heights ranged from 62 to 494 cm. DBH, the independent variable most commonly used for biomass prediction in the literature, was comparably small in this data set, ranging from 0.5 to 7.1 cm; only 120 (89%) of the trees sampled were taller than 137 cm. Total oven-dry mass ranged from 0.1 to 19.8 kg/tree.

Simple correlations between the biomass and predictor variables generally indicated the strongest associations with stem diameter, followed by crown diameter and tree height. For needle and branch biomass, correlation coefficients decreased as stem diameters were measured higher on the stem ($r = 0.98$ for D_{10} to 0.83 for DBH); for stem and total biomass, D_{10} provided the strongest simple correlations ($r = 0.98$). The relative strength of the associations for the different biomass components ranked in the following order: stem > total > branch > needle. Next to stem diameter, crown diameter had the strongest association with biomass ($r > 0.92$), and total height, the weakest ($r > 0.83$).

Scatter plots of biomass over the lower stem measures (D_0 – D_{20}) exhibited trends of increasing variance in biomass with increases in stem diameter. A natural-log transformation of both variables rendered the data conducive to the assumptions of linear regression. These relationships are illustrated for D_{10} in Fig. 1, this measure generally being representative of the results for the other lower stem measures.

Table 1. Characteristics of white spruce used for biomass equation construction.

	Control (<i>n</i> = 46)		Brushsaw treatment (<i>n</i> = 44)		Herbicide treatment (<i>n</i> = 45)	
	Mean	Range	Mean	Range	Mean	Range
<i>D</i> ₀ (cm)	4.8	1.6–9.9	5.6	2.3–9.5	6.0	1.7–11.4
<i>D</i> ₁₀ (cm)	4.2	1.5–9.1	5.1	1.8–8.7	5.3	1.5–10.3
<i>D</i> ₁₅ (cm)	4.1	1.5–8.9	4.9	1.8–8.4	5.2	1.4–10.1
<i>D</i> ₃₀ (cm)	3.9	1.3–8.6	4.7	1.6–8.3	4.9	1.0–9.4
DBH (cm)	2.6	0.6–7.1	2.9	0.9–5.4	2.8	0.5–6.1
HT (cm)	253	94–494	250	95–417	250	62–423
CD (cm)	135	54–240	144	66–236	144	36–262
Needle ODM (kg)	1.1659	0.0772–6.0572	1.6193	0.1333–4.3350	1.9073	0.0567–9.4926
Branch ODM (kg)	0.6488	0.0244–4.0369	0.9338	0.0486–3.0140	1.1352	0.0165–6.2085
Stem ODM (kg)	0.7362	0.0408–4.2953	0.9362	0.0637–2.4559	1.0936	0.0281–4.1487
Total ODM (kg)	2.5508	0.1454–14.3894	3.4893	0.2456–9.7269	4.1361	0.1013–19.8498

Note: *D*₀, *D*₁₀, *D*₁₅, *D*₃₀, diameter at 0, 10, 15, and 30 cm above groundline, respectively; DBH, diameter at breast height; HT, height; CD, crown diameter; ODM, oven-dry mass.

In general, eq. 3 provided a reasonable fit to the data from all the aboveground biomass components and measures of lower stem diameter ($r^2 > 0.95$; Table 2). All four lower stem measures performed similarly. Regression coefficients of variation (CV, standard error of the estimate, expressed as a percentage of mean biomass) are similar, but rank as follows: 24.1% for total biomass < 27.2% for stem biomass < 27.6% for needle biomass < 28.6% for branch biomass. Figure 2 illustrates the fit of eq. 3 to total aboveground biomass and *D*₁₀ data, in arithmetic units. Both predicted values and their confidence limits have been corrected for bias using eq. 8.

In contrast to the lower stem diameters, the biomass–DBH relationships were characterized by curvilinear trends and relatively constant variance throughout the range of data sampled. A natural-log transformation induced heteroscedasticity in the data, violating regression assumptions somewhat. Nevertheless, since this model is so widely used with DBH elsewhere in the literature, fit statistics are provided for eq. 3 in Table 2, for comparison with both the lower stem relationships and other data sets. Coefficients of variation increased over the lower stem relationships, ranging from 25% for stem biomass to 50% for branch biomass. Equation 4 provided improvements in precision; however, we found it necessary to insert an intercept term in the model for better fit, particularly for smaller trees:

$$[12] \quad M = \beta_0 + \beta_1 D^{b_1} + \epsilon$$

With this model, stem biomass estimates were the most precise (CV = 19%), followed by total, needle, and branch biomass (CV > 35%). With the possible exception of stem biomass prediction, DBH was not as reliable a predictor of the other biomass components, likely because of its relatively small range in the juvenile trees sampled.

When eqs. 3 and 11 were tested for treatment influences, only the relationships with stem biomass exhibited evidence of differences, and these were largely associated with differences between treated and untreated trees ($p < 0.08$, Table 2). It is well established that stand tending efforts change the relationship between crop tree stem diameter and height (e.g., Pitt et al. 2004) through a reduction of competition for resources. It follows that a general biomass equation based solely on stem diameter may not accurately predict across conditions where this height–diameter relationship changes.

In the sample data, the relationship between the natural log of height and the natural log of stem diameter was linear for all stem measures tested (e.g., *D*₁₀, Fig. 3). In all cases, the slope of the relationship was constant across the three tending treatments ($p > 0.16$), but model intercepts differed between treated and untreated trees ($p < 0.01$). These results suggested that models expanded to include height might be more robust and applicable under different competition conditions than the simpler models containing stem diameter alone.

Results of backward elimination of predictor variables including stem diameter, tree height, and crown diameter are summarized in Table 3. For stem biomass prediction, the D^2HT term in eq. 6 was significant ($p < 0.01$) and greatly improved (>45%) precision over the simpler eq. 3, regardless of the lower stem diameter measure used. Coefficients of variation between 13% and 16% reflect the highest prediction precisions observed in this study. Crown diameter, while strongly correlated with stem biomass, did not contribute significantly to a model already containing stem diameter and, therefore, did not enter any of the equations. Treatment influences on these improved equations could not be detected ($p > 0.19$), suggesting that including tree height in the model largely accounted for the unexplained treatment variation present in eq. 3.

For *D*₀–*D*₁₅, total aboveground biomass estimation improved marginally (>7%) by including total tree height in eq. 3 (Table 3). This gain is generated by, and proportional to, the contribution of stem biomass to total biomass. For the same lower stem measures, the addition of crown diameter in eq. 3 improved the precision of branch biomass estimates between 5% and 8%. For all the lower stem diameter measures, eq. 3 could not be improved upon for needle biomass estimation.

For DBH, the best fitting nonlinear regression model tested was the modified Honer's eq. 7 (Table 3). This model, which includes tree height, provided >6% gains in precision over eq. 11 for all biomass components, including needle and branch estimates. Despite these gains, however, model RMSEs were more than 38% higher than the RMSEs of models involving the lower stem diameter measures, reflecting the overall weakness of using this measure for predictions of juvenile biomass.

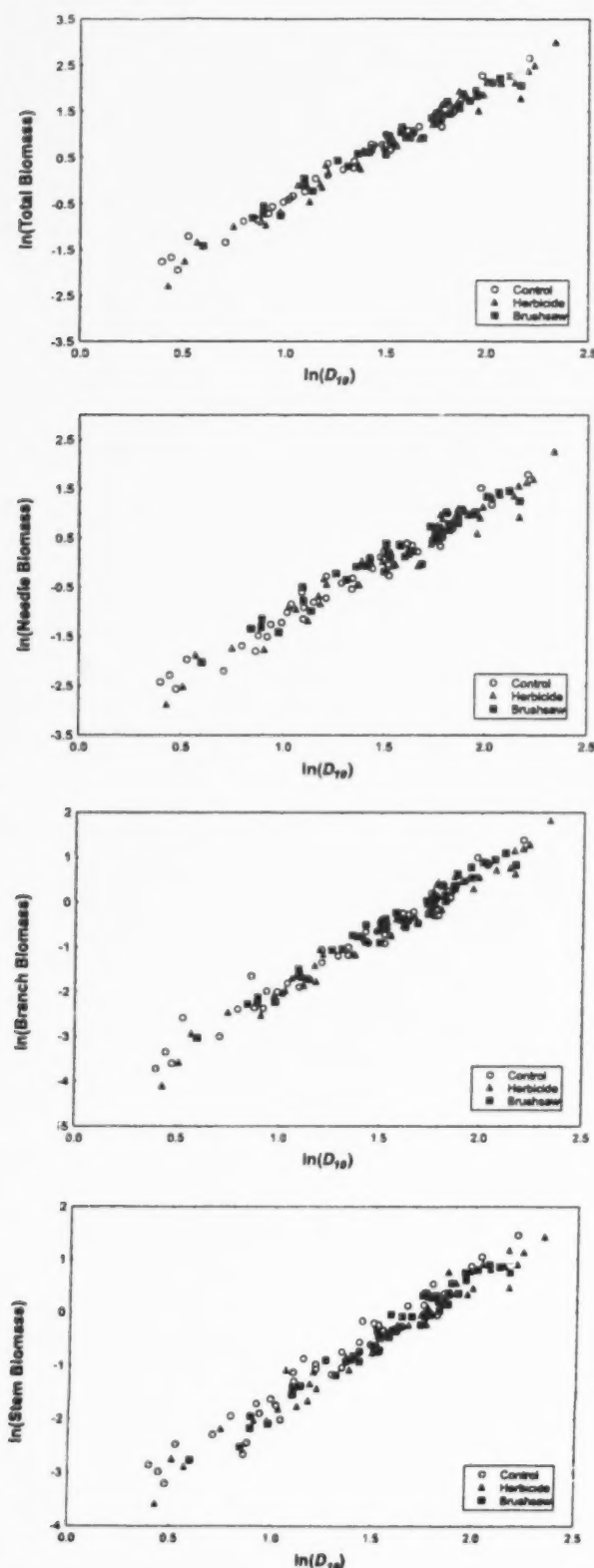


Fig. 1. Aboveground biomass components versus basal diameter at 10 cm above groundline (D_{10}), in natural-log units.

Mean individual-tree and per-hectare biomass estimates for spruce at Fallingsnow, based on independent data, are summarized in Tables 4 and 5, respectively. Individual spruce in herbicide-treated plots contained twice as much aboveground biomass as untreated spruce and one-third more biomass than brushsaw-treated spruce. These differences translated into even wider margins on a per-hectare basis, with treated plots supporting nearly 5000 to 7000 kg/ha of total spruce biomass, compared with only 2500 kg/ha in control plots. Such differences between treatments were decisive enough that ANOVA outcomes did not vary among biomass estimation models. For individual tree comparisons, treated plots and control plots differed ($p < 0.01$), as did herbicide and brushsaw plots ($p = 0.02$); on a per-hectare basis, treated plots differed from control plots ($p = 0.02$), whereas herbicide and brushsaw plots contained similar spruce biomass ($p > 0.11$).

As expected from the previous analyses conducted on the regression data, parameterizing eq. 3 to account for treatment differences produced needle and branch biomass estimates that differed little ($\leq 2\%$) from estimates generated from equations based solely on diameter. With stem biomass, however, stem diameter alone (eq. 3) underestimated untreated spruce stem biomass by 10% and overestimated values in the brushsaw and herbicide treatments by 1% and 6%, respectively. Models including height generally produced stem and total biomass estimates that were similar to those of the treatment-parameterized models, confirming earlier evidence that height, as an independent variable, provides model flexibility across different competition levels. Important from an experimental point of view, models containing height as an independent variable consistently lead to stem and total biomass estimates that had the lowest standard errors. Of course, this increased statistical power offered little advantage in this study, where treatments diverged so widely.

Discussion and conclusions

Aboveground biomass components of juvenile plantation white spruce could readily be predicted from a variety of measures of stem diameter, with levels of precision similar to those made for older stands in other studies found in the literature (Ter-Mikaelian and Korzukhin 1997). With lower stem measures, total biomass had the highest prediction precision with CV (standard error of the estimate, expressed as a percentage of mean biomass) equal to 24%, followed by stem biomass at 27%, and needle and branch biomass at 28% and 29%, respectively. With the exception of stem biomass, diameter at breast height (DBH) provided less prediction precision on these 10-year-old trees than the lower stem diameters ($CV > 35\%$). Harding and Grigal (1985) report the only biomass equations we found in the literature for plantation-grown white spruce. For trees ranging in age from 19 to 43 years, their model CVs compare at 15%, 22%, 44%, and 33% for total, stem, needle, and branch biomass, respectively. For naturally regenerating juvenile white spruce, Ter-Mikaelian and Parker (2000) also report similar model prediction CVs at 25%, 23%, 27%, and 33% for the

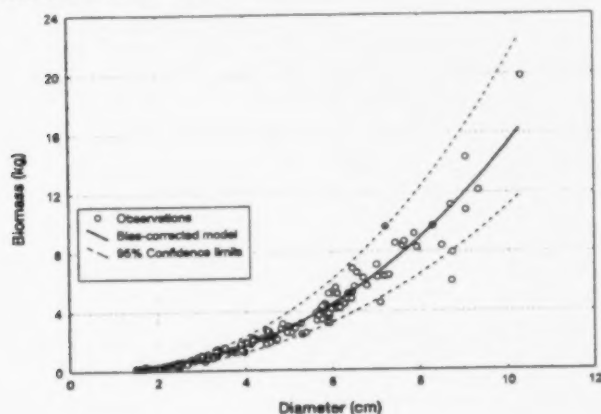
Table 2. Statistics for the regression of biomass (kg/tree) on stem diameter (cm) (eq. 3, back transformed to arithmetic units).

Diameter	Biomass component	b_0	b_1	b_2	r^2	RMSE (kg)	CV (%)	Bias correction factor	SE b_0	SE b_1	SE b_2	p treatment	p treatment vs. control	p herbicide vs. brushsaw
D_0 ($n=135$)	Total	0.0407	2.4354	—	0.978	0.8315	24.6	1.0136	0.0030	0.0319	—	0.27	0.45	0.16
	Needle	0.0226	2.3401	—	0.966	0.4298	27.5	1.0193	0.0023	0.0432	—	0.85	0.89	0.60
	Branch	0.0067	2.6747	—	0.972	0.2673	29.6	1.0209	0.0008	0.0516	—	0.24	0.16	0.29
D_{10} ($n=135$)	Stem	0.0114	2.4174	—	0.951	0.2530	27.5	1.0307	0.0006	0.0416	—	0.01	0.01	0.18
	Total	0.0586	2.4105	—	0.979	0.8125	24.0	1.0130	0.0039	0.0311	—	0.60	0.58	0.51
	Needle	0.0322	2.3113	—	0.963	0.4243	27.2	1.0211	0.0035	0.0453	—	0.54	0.52	0.43
D_{15} ($n=135$)	Branch	0.0101	2.6435	—	0.970	0.2549	28.2	1.0222	0.0010	0.0463	—	0.65	0.50	0.65
	Stem	0.0160	2.4051	—	0.961	0.2605	28.3	1.0239	0.0005	0.0269	—	0.08	0.05	0.47
	Total	0.0608	2.4132	—	0.973	0.8151	24.1	1.0163	0.0047	0.0448	—	0.76	0.92	0.48
D_{30} ($n=135$)	Needle	0.0334	2.3141	—	0.958	0.4315	27.6	1.0240	0.0037	0.0550	—	0.69	0.77	0.45
	Branch	0.0105	2.6485	—	0.966	0.2570	28.4	1.0251	0.0011	0.0564	—	0.64	0.54	0.52
	Stem	0.0167	2.4057	—	0.955	0.2534	27.5	1.0282	0.0009	0.0396	—	0.13	0.08	0.53
DBH ($n=121$)	Total	0.0819	2.3204	—	0.976	0.8016	23.7	1.0144	0.0114	0.0725	—	0.82	0.96	0.62
	Needle	0.0447	2.2201	—	0.957	0.4359	27.9	1.0248	0.0080	0.0800	—	0.84	0.82	0.66
	Branch	0.0146	2.5448	—	0.968	0.2556	28.3	1.0238	0.0024	0.0825	—	0.76	0.63	0.46
DBH (eq. 11)	Stem	0.0221	2.3236	—	0.966	0.2331	25.3	1.0209	0.0018	0.0598	—	0.08	0.03	0.02
	Total	0.8812*	1.2878*	—	0.780	1.4694	38.9	1.0964	0.0831	0.0501	—	0.01	0.07	0.06
	Needle	0.4391*	1.2132*	—	0.719	0.7524	43.2	1.1198	0.0471	0.0531	—	0.04	0.17	0.17
DBH (eq. 11)	Branch	0.2029*	1.3775*	—	0.728	0.4999	49.6	1.1494	0.0234	0.0600	—	0.09	0.16	0.05
	Stem	0.2257*	1.3467*	—	0.871	0.2564	25.0	1.0545	0.0139	0.0380	—	0.02	0.03	0.05
	Total	0.8202	0.2741	2.0676	0.833	1.3054	35.3	—	0.0982	0.0591	0.2256	0.11	0.19	0.23
DBH (eq. 11)	Needle	0.4366	0.1276	2.0261	0.904	0.6960	40.9	—	0.0496	0.0368	0.2918	0.10	0.19	0.12
	Branch	0.2160	0.0582	2.2392	0.773	0.4555	46.1	—	0.0331	0.0139	0.3270	0.27	0.26	0.42
	Stem	0.1616	0.0933	1.9585	0.948	0.1924	19.9	—	0.0173	0.0123	0.0805	0.05	0.06	0.21

Note: Statistics for eq. 11 are also shown for DBH, D_{10} , D_{15} , D_{30} , diameter at 0, 10, 15, and 30 cm above groundline, respectively; DBH, diameter at breast height; CV, coefficient of variation; RMSE, root mean square error; p treatment, p value for the hypothesis of equal regression relationships among treatments, based on multivariate analysis of intercept and slope parameters; p treatment vs. control, p value for the contrast of regression relationships between treated (herbicide + brushsaw) and untreated (control) plots; p herbicide vs. brushsaw, p value for the contrast of regression relationships between herbicide and brushsaw treatments.

*Provided for comparison only. The model did not satisfy ordinary least squares assumptions for homogeneity of variance.

Fig. 2. Total aboveground biomass versus basal diameter at 10 cm above groundline (D_{10}) with eq. 3 predictions and confidence limits. Both total aboveground biomass and D_{10} have been transformed to arithmetic units and corrected for bias with eq. 8. See Table 2 for fit statistics.

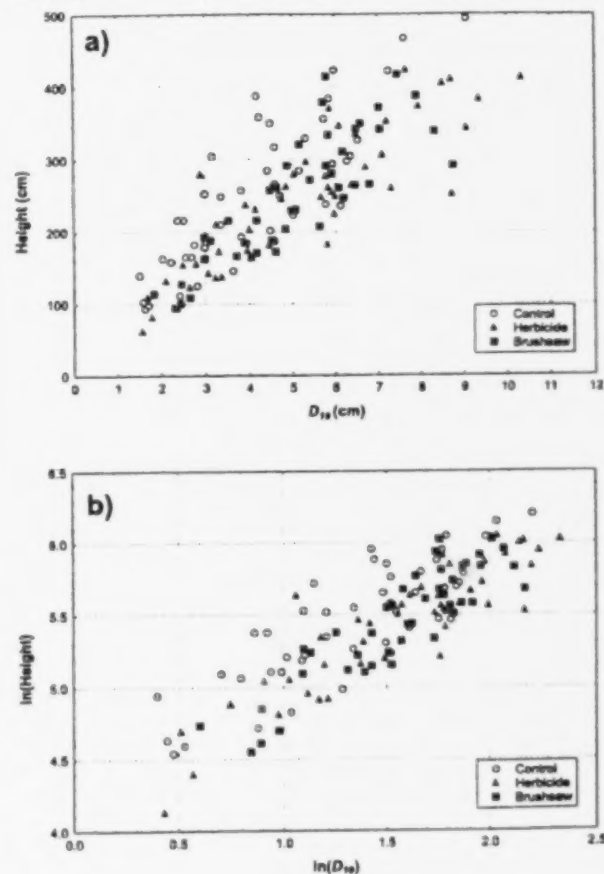


same components. Other white spruce studies involve older natural stands and report comparable estimation precisions for stem and total biomass, but branch and needle estimates are frequently less precise than those reported herein. Alemdag (1983), for example, reports CVs of 85% and 88% for branch and needle biomass in mature white spruce.

Several studies have concluded that height, as an independent variable, adds only marginal precision to the predictive capacity of diameter-based biomass regressions (Jenkins et al. 2003; Wagner and Ter-Mikaelian 1999; Ter-Mikaelian and Korzukhin 1997). In this investigation, the addition of height as an independent variable reduced the standard error of the estimate for stem and total biomass by an average of 48% and 8%, respectively, for lower stem measures, and 7% and 8%, respectively, for DBH. Harding and Grigal (1985) found nearly identical improvements in older plantation white spruce: 48% and 9% for stem and total biomass, respectively. Ter-Mikaelian and Parker (2000) found that height improved the precision of stem biomass estimates in natural juvenile spruce by only 10%. Both these latter studies found needle and branch biomass models invariant to the addition of height, consistent with our results.

Some white spruce studies suggest the addition of height as an independent variable as a means of adjusting for effects such as stand age, density, and site quality (e.g., Ker and van Raalte 1981). In this study, white spruce growing under tended and untended conditions were characterized by different height-diameter relationships that were not reflected by stem biomass equations based solely on diameter. For a specific situation, one can generate separate "treated" and "untreated" biomass equations (e.g., Ter-Mikaelian and Parker 2000), but a more generic approach is desirable if the equations are to have potential application elsewhere. In this study, including height in the estimation of stem and total biomass accounted for variation associated with the stand tending treatments tested, rendering more robust equations that may have potential for application to juvenile planted white spruce elsewhere, given, of course, the cautions cited by Crow and Schlaegel (1988). On a per-hectare basis, plots

Fig. 3. Stem height versus basal diameter at 10 cm above groundline (D_{10}) in arithmetic units (a) and in natural-log units (b).



tended with brushsaws or herbicide contained two to three times the spruce biomass of untreated plots ($p = 0.02$). With such wide differences among treatments, use of equations based solely on stem diameter, which underestimated untreated stem biomass and overestimated treated stem biomass, had little effect on statistical power to detect treatment differences. However, in applications where treatment differences are more subtle, statistical power may be compromised if both stem diameter and tree height are not used as predictor variables. The relationship between needle or branch biomass and stem diameter did not appear to be influenced by the vegetation management treatments.

White spruce crown diameter was highly correlated with measures of lower stem diameter ($r > 0.92$), suggesting its potential use as a surrogate for stem diameter measurements in biomass estimates made from remote sensing applications (e.g., Pouliot et al. 2002). Because of its strong correlation with stem diameter, however, crown diameter generally did not contribute significantly to models already containing the former. An exception was branch biomass, where the addition of crown diameter increased estimation precision by about 8%. This result seems logical, since larger crowns must certainly be supported by more branches. Ker and van

Table 3. Improved biomass equations based on inclusion of tree height (HT) and (or) crown diameter (CD) (all parameters significant at $\alpha = 0.01$).

Diameter	Biomass component	Equation (all units in cm)	Equation No.	r^2	RMSE (kg)	CV (%)	% improvement	p treatment	p treatment vs. control	p herbicide vs. brushsaw
D_0 ($n=135$)	Total	$(0.0154D_0^{2.257} \times HT^{0.239}) \times 1.0123$	5	0.980	0.7732	22.8	7.0	0.54	0.25	0.94
	Needle	No improvement found	3	0.966	0.4298	27.5	0.0	0.85	0.89	0.60
	Branch	$(0.0012D_0^{3.182} \times CD^{0.431}) \times 1.0188$	5	0.975	0.2508	27.7	6.2	0.80	0.76	0.68
	Stem	$[0.0003(D_0^2 \times HT)^{0.8667}] \times 1.0137$	6	0.979	0.1465	15.9	45.2	0.19	0.22	0.13
D_{10} ($n=135$)	Total	$(0.0256D_{10}^{2.600} \times HT^{0.1929}) \times 1.0122$	5	0.980	0.7401	21.9	8.9	0.35	0.23	0.67
	Needle	No improvement found	3	0.963	0.4243	27.2	0.0	0.54	0.52	0.43
	Branch	$(0.0023D_{10}^{2.348} \times CD^{0.3970}) \times 1.0209$	5	0.972	0.2350	26.0	7.8	0.78	0.52	0.92
	Stem	$[0.0004(D_{10}^2 \times HT)^{0.8618}] \times 1.0101$	6	0.984	0.1285	13.9	50.1	0.99	0.99	0.98
D_{15} ($n=135$)	Total	$(0.0222D_{15}^{2.205} \times HT^{0.2339}) \times 1.0150$	5	0.976	0.7457	22.0	8.5	0.47	0.48	0.35
	Needle	No improvement found	3	0.958	0.4315	27.6	0.0	0.69	0.77	0.45
	Branch	$(0.0020D_{15}^{2.3156} \times CD^{0.423}) \times 1.0234$	5	0.969	0.2439	27.0	5.1	0.79	0.51	0.96
	Stem	$[0.0004(D_{15}^2 \times HT)^{0.8630}] \times 1.0125$	6	0.980	0.1291	14.0	49.1	0.97	0.82	0.97
D_{30} ($n=135$)	Total	No improvement found	3	0.976	0.8016	23.7	0.0	0.82	0.96	0.53
	Needle	No improvement found	3	0.957	0.4359	27.9	0.0	0.84	0.82	0.62
	Branch	No improvement found	3	0.968	0.2556	28.3	0.0	0.76	0.63	0.66
	Stem	$[0.0006(D_{30}^2 \times HT)^{0.8360}] \times 1.0103$	6	0.981	0.1187	12.9	49.1	0.99	0.85	0.99
DBH ($n=121$)	Total	$0.7567 + [(DBH^{2.6381})/(15.0930 - (2264.8/HT))]$	7	0.856	1.2192	32.9	6.6	0.29	0.17	0.39
	Needle	$0.3961 + [(DBH^{2.5917})/(31.9643 - (4799.6/HT))]$	7	0.795	0.6546	38.4	6.0	0.50	0.55	0.58
	Branch	$0.1027 + [(DBH^{2.4255})/(33.0168 - (4249.9/HT))]$	7	0.803	0.4267	43.2	6.3	0.98	0.95	0.86
	Stem	$0.1075 + [(DBH^{2.2328})/(23.7834 - (2844.6/HT))]$	7	0.955	0.1778	17.6	7.6	0.30	0.43	0.20

Note: D_0 , D_{10} , D_{15} , D_{30} , diameter at 0, 10, 15, and 30 cm above groundline, respectively; DBH, diameter at breast height; CV, coefficient of variation; RMSE, root mean square error; % improvement, reduction in RMSE for equation based on stem diameter alone (Table 2); p treatment, p value for the hypothesis of equal regression relationships among treatments, based on multivariate analysis of model parameters; p treatment vs. control, p value for the contrast of regression relationships between treated (herbicide + brushsaw) and untreated (control) plots; p herbicide vs. brushsaw, p value for the contrast of regression relationships between herbicide and brushsaw treatments.

Table 4. Estimated treatment means for individual white spruce biomass (kg/tree) on Fallingsnow Ecosystem Project plots.

Biomass component	Equation No., independent variable(s)	Control	Brushsaw treatment	Herbicide treatment	SE	RMSE
Needle	3, D_{10}	1.19	1.67	2.33	0.094	1.361
	3, D_{10} , by treatment	1.20	1.68	2.27	0.093	1.345
Branch	3, D_{10}	0.65	0.95	1.41	0.066	0.948
	3, D_{10} , by treatment	0.66	0.96	1.39	0.066	0.957
Stem	3, D_{10}	0.69	0.98	1.39	0.059	0.849
	3, D_{10} , by treatment	0.76	0.97	1.32	0.058	0.835
	6, D_{10} , HT	0.78	0.95	1.24	0.055	0.796
Total	3, D_{10}	2.53	3.60	5.11	0.216	3.118
	3, D_{10} , by treatment	2.61	3.62	4.95	0.214	3.095
	5, D_{10} , HT	2.60	3.58	4.99	0.213	3.076
<i>n</i>		175	245	246		

Note: SE, standard error of the estimated treatment mean (kg/tree); RMSE, root mean square error from ANOVA (kg/tree); D_{10} , stem diameter at 10 cm above groundline; HT, height; *n*, number of trees per treatment.

Table 5. Estimated treatment means for white spruce biomass (kg/ha) on Fallingsnow Ecosystem Project plots.

Biomass component	Equation No., independent variable(s)	Control	Brushsaw treatment	Herbicide treatment	SE	RMSE
Needle	3, D_{10}	1153	2272	3180	315	546
	3, D_{10} , by treatment	1170	2290	3105	322	558
Branch	3, D_{10}	635	1295	1928	210	363
	3, D_{10} , by treatment	643	1310	1903	215	372
Stem	3, D_{10}	672	1339	1906	194	335
	3, D_{10} , by treatment	737	1324	1797	179	310
	6, D_{10} , HT	757	1290	1688	152	263
Total	3, D_{10}	2459	4897	6979	710	1230
	3, D_{10} , by treatment	2534	4931	6771	707	1224
	5, D_{10} , HT	2531	4871	6815	676	1172
Stocked quadrats (%)		39	54	55		

Note: SE, standard error of the estimated treatment mean (kg/ha); RMSE, root mean square error from ANOVA (kg/ha); D_{10} , stem diameter at 10 cm above groundline; HT, height.

Raalte (1981) reported similar findings in both branch and foliage biomass estimates for natural white spruce.

The question of whether or not existing equations could have been satisfactorily applied to spruce at Fallingsnow demands attention. As previously mentioned, all studies reported in the literature were conducted on stands that were old enough to have reached crown closure. The spruce at Fallingsnow, not having reached this stage at age 10, represented an extrapolation scenario for any of the existing equations. Table 6 summarizes estimates made from five different sets of equations published in the literature, for a tree with DBH of 6 cm and HT of 405 cm. We chose this tree size to be near the upper end of our sampled size range, yet overlapping the lower end of the sample ranges of the other studies. Crow and Schlaegel (1988) suggest averaging estimates from a number of sources when extrapolating equations to new areas, and it appears that doing so might have proven successful in the estimation of spruce stem biomass at Fallingsnow. However, existing equations would have underestimated branch, needle, and, correspondingly, total biomass by 68%, 75%, and 56%, respectively. Clearly, a lack of

self-pruning on these young spruce affected branch/stem and needle/stem ratios, a situation that must be captured by equations if accurate estimates are required for juvenile stands. Indeed, plantation-grown white spruce tend to retain their branches longer than natural white spruce, and this is reflected in Harding and Grigal's (1985) predictions, which have much higher branch and foliage estimates per unit of stem biomass than any of the natural stands.

In contrast, naturally regenerating white spruce in a shelterwood understory might be expected to have a higher proportion of branch biomass to foliar biomass relative to more open-grown plantation trees. Ter-Mikaelian and Parker's (2000) equations estimate total, stem, branch, and needle biomass for a 6 cm DBH tree (estimated 10 cm at D_0) at 12.2, 3.3, 6.4, and 3.9 kg, respectively, overestimating branch biomass and underestimating foliar biomass relative to our trees. We therefore agree with the caution that biomass estimates may vary from site to site with stand conditions (Crow and Schlaegel 1988) and further assert that equations should be specific to planted versus natural stands, as well as immature versus mature stands.

Table 6. Comparison of estimates of aboveground biomass components (kg/tree) for white spruce, based on a diameter at breast height (DBH) of 6 cm and a height of 405 cm.

Source	Total aboveground	Stem	Branch	Needles	DBH range	Location
Ker 1980*	6.3	3.6	1.5	1.2	2.1–32.3	Natural, Nova Scotia
Lavigne and Nostrand 1981	6.3	3.0	0.8	2.5	3.0–30.5	Natural, Newfoundland
Freedman et al. 1982	7.2	5.2	2.0	1.8	1.5–29.5	Natural, Nova Scotia
Alemdag 1983	2.7	2.0	0.2	0.2	6.3–35.8	Natural, central Ontario
Harding and Grigal 1985	6.0	2.2	2.6	2.0	1.1–32.6	Plantation, Lake States (Minn.)
Mean	5.6	3.4	1.1	1.4		
Fallingsnow	12.6	3.4	3.5	5.6	0.5–7.1	Plantation, northwestern Ontario

*Only DBH was used as an independent variable.

In conclusion, this study reveals that along with obvious site and age differences, three additional points of caution should be considered before extrapolating any existing biomass equations to data outside of those upon which the equations were constructed:

- (1) The widely used diameter at breast height (DBH) may not be as good as basal stem diameter in predicting biomass in younger stands.
- (2) Stem and total biomass equations should contain both stem diameter and height as independent variables to compensate for varying competition levels in younger stands.
- (3) Branch and foliage biomass equations should be calibrated for plantations and, in particular, pre-crown closure stand conditions, when applicable.

Acknowledgements

This project was funded by the Ontario Ministry of Natural Resources (OMNR). Amy Bolduc, Ray Ferguson, Darren Derbowka, John Ralston (OMNR), and Adam Warren (Notre-Dame-Des-Grand-Lacs) provided valuable technical support. We also thank Michael Ter-Mikaelian (OMNR), Michael Weber (Canadian Forest Service), and three anonymous reviewers for valuable comments on previous versions of this manuscript.

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